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ON THE ANATOMY OF *GRYLLOBLATTA CAMPODEIFORMIS* WALKER

5. THE ORGANS OF DIGESTION[1]

BY E. M. WALKER[2]

Abstract

The digestive organs of *Grylloblatta* resemble those of the orthopteran suborder Ensifera but differ strikingly in the cuticle and epithelium lining the proventriculus, in which there are 12 similar longitudinal divisions characterized by rows of flexible, backwardly directed lamellae, in place of the six divisions of the Ensifera armed with columns of complex sclerotized teeth. The proventricular collum is much longer than in any of the Ensifera; the two gastric caeca of the latter are represented by a single bilobed sac; the malpighian vessels are fewer than 30 and are simply arranged; and the salivary glands are very compact, appearing like a single organ.

As a main conclusion to this and the previous papers of this series the following views are advanced:

(1) The Grylloblattaria, although cursorial, are the nearest relatives of the Ensifera, but differ from the latter group too widely to be included within it.

(2) The saltatorial habit has been independently evolved in the Ensifera and Caelifera.

A summary is given of the main views on the function of the proventriculus in mandibulate insects, particularly the orthopteroid forms. The proventriculus of *Grylloblatta* is believed to serve as a regulatory valve and also possibly as a propulsive organ for the movement of food along the digestive tract.

Introduction

The present study of the digestive organs of *Grylloblatta* is based upon even scantier material than were the previous parts of this series, viz., a few dissections chiefly of adult individuals and a single series of sections of a male nymph, about 10 mm. long, which was made many years ago by my wife.* This specimen was fixed in Carnoy's fluid, embedded in paraffin, and cut into sections 15μ in thickness. Two combinations of stains were used, Heidenhain's iron haematoxylin with orange G for about three-fifths of the series, and Delafield's haematoxylin with eosin for the remainder. The former stain gave slightly the better results of the two.

Much has been written on the digestive organs of insects, and the orthopteroid orders, being relatively primitive groups, have received an ample share

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of attention. Following Dufour's (20) general survey of the anatomy of the old Order Orthoptera (together with Hymenoptera and Neuroptera), the next important general treatise on the anatomy of the digestive organs of these insects is that of Bordas (12). This is still a useful general survey of the gross anatomy of the alimentary canal and its appendages in the main groups of orthopteroid insects, treated from the comparative standpoint. Bordas also dealt with some of the families in greater detail, viz., the Forficulidae (5), Gryllidae (8, 9, 12), Phasmidae (7), Acrididae (10), and Blattidae (6, 9), besides publishing many papers on special features of the anatomy and histology of the alimentary canal and its associated glands.

Numerous papers by other authors on the anatomy and physiology of the digestive system of insects appeared in the last quarter of the nineteenth century, including a considerable number on the function of the proventriculus, in which opposing views were presented. Reference will be made later to some of these when the function of the proventriculus of *Grylloblatta* is considered.

During the twentieth century the digestive organs of the Isoptera have become well known through the writings of Imms (31), Holmgren (30), and Sutherland (49), and the inner structure of the proventriculus has been recently described by Judd (33) in the genus *Termopsis*. While possessed of certain peculiar features associated with their xylophagous habits, the alimentary canal in this order is sufficiently like that of the Blattodea to be in accord with the now generally accepted view of the Isoptera as an order of orthopteroid insects.

Until the third decade of the present century two small families of Saltatoria, viz., Tridactylidae and Cylindrachetidae, were generally placed by taxonomists in the Grylloidea, owing to their superficial resemblance to the Gryllotalpidae. Dufour (20) had already recognized that the affinities of *Tridactylus* were with the Acridoidea, particularly the genus Tetrix, basing his view on the characters of the alimentary canal and the reproductive organs. Walker (52) noted the similarity between the ovipositors of *Rhipipteryx*, another genus of Tridactylidae, and the Acridoidea. But the majority of taxonomists continued to treat these families as specialized Gryllidae or at least Ensifera, until the detailed studies of Carpentier (14, 15, 16, 17), Ander (1), and Fernando (24) appeared. These studies, in which the alimentary canal of both *Tridactylus* and *Cylindroryctes* are described, present evidence amounting virtually to proof, of the view that these two families are nearly related to one another, and belong to the same suborder as the Acridoidea, this suborder being now known as the Caelifera. The recent comparative studies of the proventriculus of orthopteroid insects by Judd (33) add still further evidence of the soundness of these conclusions.

Other important advances in orthopterology have been made during this century, which throw light on the phylogeny of the major groups through our increasing knowledge of the fossil record, as well as through more critical study of the anatomy of living forms. Handlirsch's (26) monumental work

on fossil insects remains the foundation for all future studies in this field. Zeuner (60) in his exhaustive treatise on the fossil Ensifera has traced this group back to certain protorthopteran families of the Upper Carboniferous period and believes that the Acridoidea and their nearest relatives (later termed the Caelifera by Ander) were derived by a separate line of descent from nearly related protorthopteran families of the same period. Ander (2, 3) approaching the problem from the standpoint of comparative anatomy of recent Ensifera, supports Zeuner's view that the Ensifera and Caelifera represent distinct lines of descent at least as far back as the Upper Carboniferous and emphasizes the impossibility of deriving the Caelifera from the Ensifera. His main objective, however, is to determine the interrelationships of the various families of Ensifera, and in this phase of the subject his views differ considerably from those of Zeuner. They are, however, of significance here only in so far as it is possible to determine what are the primitive characteristics of the Ensifera. Ander's scholarly study is the most important work from our point of view that has yet appeared, since it is based not merely upon one or two sets of characters, but upon a consideration of the anatomy as a whole.

It may be added that, during the present century, a number of comprehensive textbooks have appeared in which useful summaries of the structure of the alimentary canal are given. Among these may be specially mentioned Berlese (4), Imms (32), Deegener (19), Weber (57), and Snodgrass (48). We have found Snodgrass the most generally useful for the purpose of the present paper, and the terminology employed therein has been followed as closely as possible.

The Preoral Cavity

The space usually known as the "mouth cavity" or "buccal cavity" has been more correctly designated as the *preoral cavity* by Snodgrass (48), since it lies wholly external to the true mouth. It is the space enclosed by the mouth parts, being bounded in front (or above) by the labrum, behind (or below) by the labium, and laterally by the mandibles and maxillae. These parts have been already described for *Grylloblatta* in Part 1 of this series (Walker, 53).

Since *Grylloblatta* is a prognathous insect, the preoral cavity opens (by the food meatus, Snodgrass (48)) at the anterior extremity of the ventral surface of the head. The epipharyngeal surface of the labrum and clypeus form its roof rather than its anterior wall (as in most Orthoptera), while the labium forms its floor rather than its posterior wall (Fig. 2). Apart from these differences from the majority of Orthoptera in its relations to the horizontal axis of the head, the preoral cavity of *Grylloblatta* conforms to Snodgrass's description as applied to Orthoptera in general. It is bounded laterally by the mandibles and maxillae, which are directed forward, and distally curved somewhat ventrad. It is divided by the hypopharynx (Figs. 1, 2, *hy*) into a

salivary chamber below, and a food passage above, the latter space opening immediately behind the labrum and between the apical parts of the mandibles in the food meatus.

The salivary chamber or *Salivarium* (Figs. 1, 2, *sv*) is a simple pocket between the hypopharynx and the prementum of the labium (*pm*). There is no salivary cup, the orifice of the salivary duct being a simple median aperture at the posterior limit of the pocket.

The food passage leads from the food meatus to the *Cibarium* (Figs. 1,2, *cb*), which is floored by the concave upper surface of the basal part of the hypopharynx, and is roofed by the epipharyngeal surface of the clypeus.

A pair of muscles, the *dilators of the cibarium* (Fig. 2, *dcb*) were overlooked in Part 1 of this series. These muscles arise in the base of the dorsal wall of the clypeus and pass anteroventrad to their insertion on the dorsal wall of the cibarium.

Another muscle overlooked in Part 1 is the single median *compressor of the labrum* (Fig. 2, *clr*), which arises on a small area on the base of the dorsal wall of the labrum, its fibers diverging ventrad to their insertion on the epipharyngeal wall of the labrum.

At the base of the hypopharynx, flanked by the bases of the mandibles, is the true *mouth* (*m*), from which the alimentary canal extends backwards.

The Labial or Salivary Glands and Their Ducts (Figs. 1-5)

The salivary orifice already mentioned is the opening of the median or common duct of the labial glands (Figs. 1–3, *msd*), which in *Grylloblatta* is a short, somewhat dilated chamber lying immediately above the mentum of the labium, and apparently functioning as a salivary reservoir, there being no other chamber which could serve this purpose. From this common outlet two slender *salivary ducts* (*sd*) proceed backwards from the region of the mentum into that of the submentum. Here they lie immediately beneath the suboesophageal ganglion, but, on entering the cervical region, they pass dorsally to the ventral nerve cords, as the latter leave the ganglion and take up a position just beneath the oesophagus to which they are closely applied, From here backwards they diverge and, in sections through the prothorax. may be observed close to the lateral walls of the oesophagus, passing gradually dorsad until they enter the substance of the labial glands (Fig. 4).

The usually paired *labial glands* (*sgl*) are, in *Grylloblatta*, so closely applied to one another that they appear throughout the greater part of their length as a single compact glandular mass lying on the dorsal wall of the oesophagus in the prothorax (Figs. 1, 4). Approaching the mesothorax this glandular mass sinks ventrad on the sides of the oesophagus (Fig. 5), to which it is closely applied, and still farther back in the mesothorax these ventrolateral extensions meet below, the oesophagus being for a short distance completely surrounded

by the glandular tissue. Towards the posterior limit of the mesothorax, only the ventral parts of the gland remain, and here the right and left portions are narrowly separated.

The ducts of the labial glands, entering the substance of the glands, break up into numerous canaliculi surrounded by the somewhat irregular acini (Fig. 5). The cells of the acini are large, with basally situated nuclei, which are somewhat flattened or irregular in form, and very deeply stained, no details of structure being visible in the sections. The cytoplasm is irregularly stained, the accumulations of secretion giving it a more or less vacuolated appearance towards the inner borders of the cells. In many cases drops of secretion may be seen entering the canaliculi.

The Alimentary Canal (Fig. 8)

The alimentary canal may be described under its three primary divisions, the stomodaeum, mesenteron, and proctodaeum.

The Stomodaeum

The *stomodaeum* consists of five divisions, the buccal cavity, the pharynx, the oesophagus, the crop or ingluvies, and the proventriculus.

The *buccal cavity* (Fig. 1) is a very short section of the stomodaeum, having a slight dorsoposterior curvature, as it leads to the pharynx, from which it does not differ in structure. It is that portion of the stomodaeum on which are inserted the first pair of dilator muscles termed in Part 1 (Walker, 53) the *dorsal dilators* of the buccal cavity (Muscle No. 3. See Part 1, Plate III, Fig. 27). These muscles in *Grylloblatta* arise on the base of the labrum instead of the clypeal wall, the latter being the usual site of attachment in generalized insects according to Snodgrass (48). They are omitted in Fig. 2 of the present paper. The buccal cavity passes into the pharynx at the anterior end of the frontal ganglion.

The *pharynx* as defined by Snodgrass (48) is "that part of the stomodaeum whose dorsal dilator muscles take their origin on the frontal and dorsal areas of the head wall, and are inserted posterior to the frontal ganglion and its connections". This definition applies to *Grylloblatta*, which possesses three pairs of dorsal dilators, except in so far as the first two pairs of dilators (Walker (53), Pl. III, Fig. 27) are inserted laterad of the frontal ganglion, rather than behind it. The third pair (8) is inserted behind the cerebral ganglion, and this marks the posterior boundary of the pharynx, since the second of the two pairs of ventral dilators is inserted opposite the third dorsal pair (Walker, 53).

The pharynx extends directly backwards from the buccal cavity, which it leaves at a slight bend (Fig. 2, *ph*). It is the smallest in caliber of any part of the alimentary canal. It is lined by a thin cuticle supported by a somewhat flattened epithelium, which is extensively and rather irregularly folded.

External to the basement membrane is a thin muscular layer, the inner fibers of which are longitudinal and discontinuous, the outer fibers circular and more close set. The thickness of each layer is that of a single fiber.

The *oesophagus* (Fig. 1, 2, 4, 5, *oe*) as it proceeds from the pharynx is but little larger in diameter, and scarcely widens as it passes through the prothorax. Throughout most of this region, as already described, the oesophagus is covered by the labial glands, which, in the anterior part of the mesothorax, surround it for a short distance and terminate beneath it. In most of the specimens dissected, the oesophagus widens only very gradually until the metathorax is entered, but the extent of dilatation depends upon the volume of its contents.

The *crop* or *ingluvies* (Figs. 1–7, *cr*) is merely the expanded posterior part of the oesophagus, the expansion being mainly ventral, as in the Grylloidea, with the widest part near the posterior end, at about the third or fourth abdominal segment, where it is somewhat abruptly rounded off (Fig. 7).

The walls of the oesophagus and crop (Fig. 6) are similar throughout their combined length. The epithelium is very flat, and is longitudinally folded when not distended with food. No histological differences were found between the oesophagus and pharynx, except in the flatter epithelium of the former.

The *proventriculus* (Figs. 1, 7, 9, 10) has been described by Judd (35). It is well developed and appears externally very like that of the saltatorial suborder Ensifera, although longer than is usual in this group. It is a thick-walled muscular tube, composed of an anterior necklike region or *collum* and a posterior bulbous part, which may be termed the *bulb*. It leaves the crop dextrodorsally a little before the posterior end of the latter. The first part or collum is bent somewhat to the right and folded into an anterodextral loop, the posterior limb widening into the bulb, which lies in a depression in the roof of the ventriculus near the anterior end of that chamber.

In the collum, the lining epithelium and cuticle are arranged in 12 longitudinal folds (*a*), which are comparatively flat as they approach the bulb, but become prominent as they enter its cavity. The cuticle covering these folds is beset with minute hairlike processes, rather evenly distributed and all directed backwards.

In the bulb these 12 folds (Fig. 9) are narrowed to pointed apices and in the angular intervals between these apices an alternating series of folds (*b*) arises, which form the stout bases of 12 wedge-shaped processes (*c*), each of which is demarcated from its base by a distinct notch. Alternating with these 12 processes, and therefore in alignment with the 12 anterior folds, is a second series of processes, which are longer and more compressed than those of the first series and project into the cavity of the proventriculus a little behind the first series. These are very thin and lamellate except towards their free extremities where they are somewhat swollen. The 12 folds of this second series are again subdivided into two alternating sets of six each, differing in length and in the form of their free extremities, those of one set (*d*) being longer,

extending farther back, and having sharper apices than those of the other set (*e*). These various folds or processes are thus arranged in three overlapping rows, the first row consisting of the 12 wedge-shaped processes, overlapping the bases of the second row of six flattened processes or lamellae and this second row overlapping the third row, consisting of six longer lamellae. All of the processes are beset with fine hairs, which are longest and most abundant along their free margins and at their apices.

The circular muscles of the proventriculus form a much thicker layer than those of the other divisions of the stomodaeum (Fig. 9, 10, *cm*). The longitudinal muscles internal to the circular layer are comparatively thin, although thicker than those of the oesophagus and are broken into bundles which occupy the folds. In the bulb there are also many scattered longitudinal muscle fibers which lie external to the circular layer, including isolated fibers which pass through the haemocoele to the outer surface of the ventriculus, (Fig. 7).

The manner in which the proventriculus probably functions will be considered in the general discussion (p. 331).

The *stomodaeal valve* (Fig 10, *sti*) is the last division of the stomodaeum and is that part which projects as a circular fold into the cavity of the ventriculus and is usually termed the cardiac valve. It is rather short in *Grylloblatta* (Fig 10). The smooth cuticle which covers it can, as usual, be traced over the fold to its junction with the ventricular wall.

The Mesenteron

The mesenteron consists of a single section of the gut commonly termed the *ventriculus* or stomach. It occupies the middle region of the abdomen, being usually found in the fourth and fifth or the fifth and sixth segments. In its natural position (Fig. 1) it is bent more or less ventrad upon its junction with the proventriculus. It is a short wide sac, broadest towards its anterior end. Here there is a dorsal concavity (Fig. 7) which receives the bulb of the proventriculus, and on each side and below the depression there is a forward bulging of the wall forming a pouch which is slightly bilobed, representing an incipient pair of gastric caeca (*gc*). The ventriculus is slightly twisted so that the right caecum lies a little higher than the left. Posteriorly the ventriculus is somewhat narrowed to its junction with the intestine.

The ventricular epithelium (Figs. 10, 11) is similar throughout its extent, not being specialized in the gastric caeca. It is arranged in tall columnar folds, composed of digestive cells with groups of smaller regenerative cells at their bases. The regenerative cells, being crowded by mutual pressure, show flattened or crescentic nuclei, which are well stained, and small cytoplasmic areas. Indications of mitosis may be observed here and there. As the cells migrate toward the lumen, becoming the digestive cells, they are more elongate with elliptical nuclei, which stain more faintly the nearer they approach the lumen. The cytoplasm is more abundant and is finely granular

in appearance. There is no trace of a peritrophic membrane, a fact that is not wholly surprising in view of the apparent absence of hard particles in the food.

The epithelium in the specimen sectioned was in a state of active disintegration involving the separation of numerous fragments of cells. There is thus no indication of a striated border. The ventricular cavity is open and must have contained fluid material but there is no definite indication of the presence of solid particles.

External to the basement membrane is a thin but continuous layer of circular muscle fibers, followed by a more scattered layer of longitudinal fibers, some of which pass forward to the proventriculus as already described.

The Proctodaeum or Intestine

The intestine of *Grylloblatta* is of moderate length and follows a somewhat sinuous course with a double curvature (Fig. 1). Its two main divisions, termed by Snodgrass the anterior and posterior intestines, are sharply distinct.

At the anterior end of the intestine is a constriction which appears externally as the junction between the ventriculus and intestine. A slight thickening of the circular muscles at this constriction forms a small pyloric sphincter (Fig. 12).

The *malpighian vessels* (Figs. 8, 12, 13) open into the intestine at the pyloric constriction, just behind the sphincter muscle. They evidently vary in number, one adult female in which they were carefully counted having had 17, another 14, a third about 24, while in the series of sections made from a male nymph there appear to be only 12. They are fairly evenly distributed and close set at their junctions with the intestine. They are unbranched and of considerable length, winding both forwards and backwards throughout most of the abdominal cavity. In thickness they are nearly uniform in adults but in sections of the nymph many are considerably enlarged distally (Fig. 13).

The *anterior intestine* (Figs. 1, 8, 12, 13) is short and not divisible into ileum and colon. It generally appears to be much smaller in diameter than the ventriculus and becomes still smaller as it approaches the beginning of the posterior intestine. As it leaves the ventriculus it has a ventral position but follows a curved course to the left and then dorsad, taking another bend backwards just before joining the posterior intestine.

At the anterior end, in the serial sections, it appears in cross section (Fig. 13) and here the lining epithelium is thrown fairly symmetrically into six longitudinal folds, which continue throughout the course of the anterior intestine. Examination of the lumen in dissected specimens shows that these folds of epithelium originate just in front of the constriction, there being thus a very rudimentary pylorus or pyloric region.

The epithelium of the anterior intestine consists of columnar cells, regularly arranged, with elliptical nuclei halfway between base and apex. The cytoplasm is clear and is most dense at the inner ends, where a striated border can be seen. A thin but distinct cuticular intima covers the inner surface of the epithelium. As already noted there is a slight transverse fold of the epithelial layer at its junction with the ventricular epithelium, just in front of the pyloric constriction.

The muscularis is very thin and consists, as usual, of an inner continuous circular layer and outer longitudinal fibers which are sparse and somewhat scattered.

The *posterior intestine or rectum* (Figs. 1, 8, 15).—A distinct constriction separates the anterior and posterior intestines, which is followed by a marked increase in the diameter of the gut. This constriction marks the position of the rectal valve where the columnar epithelium of the anterior intestine forms a short but distinct backward fold before joining the flatter epithelium of the rectum. The rectum follows a straight course to the anus and is somewhat indistinctly divided into a wider anterior portion, the *rectal sac*, and a narrower posterior region, the *rectum* proper. The epithelium lining both of these regions is for the most part extremely flat and is covered by a distinct cuticle. In the rectal sac, however, there are six very prominent *rectal pads* (Figs. 1, 8, 15), about equally spaced and arranged in a partially doubled transverse series, two or three pads being in advance of the others. Each pad is broadly oval in outline, with the inner surfaces flattened, and is composed of a single layer of tall columnar epithelial cells with their oval nuclei in the inner half and the cytoplasm most dense next to the inner borders. The muscularis is thinner than usual in orthopteroid insects. The circular muscles form a thin but continuous coat, especially on the rectal sac. The longitudinal muscles consist, on the rectal sac, chiefly of six equally spaced bundles, which extend posteriorly to the anus, but on the walls of the rectum proper there are numerous, somewhat smaller bundles in the intervals between the six main bundles.

Special rectal muscles.—Owing to an insufficiency of material for satisfactory dissection, the following descriptions of muscles are subject to revision:

Retractors of the rectum (Fig. 8, *rtr*). A pair of slender bundles of parallel fibers arising on the anterior margins of the ninth tergum near its anteroventral angles, and passing mesocaudad to the lateral walls of the rectum, where they join the longitudinal fibers of the muscularis continuing to their insertion on the rectal wall close to the anus.

Dorsal dilators of the rectum (Fig. 8, *ddr*). A pair of thin fans of slender fibers arising on the anterior margins of the ninth tergum internal to the retractors of the rectum, diverging mesad very widely to their insertion on the dorsal wall of the rectum partly on the rectal sac but chiefly on the rectum proper. These fibers are supported by a thin membranous sheath.

Ventral dilators of the rectum (Fig. 8, *vdr*). A pair of small bundles of fibers arising on the ventrolateral part of the 10th tergum and passing mesad to their insertion on the ventral wall of the rectum proper.

Dorsal dilator of the anus (Fig. 8, *dda*). A short median unpaired muscle arising centrally on the 10th tergum and passing ventrad to its insertion on the dorsal wall of the rectum close to the anus.

Ventral dilators of the anus (Fig. 8, *vda*). A pair of small muscles arising on the paraproct and passing mesad to their insertion on the lateral walls of the rectum close to the anus.

Comparison with Other Orthopteroid Insects

The gross general characteristics of the digestive organs of orthopteroid insects are the following:—

The foregut is divided into buccal cavity, pharynx, oesophagus, crop, and proventriculus. The oesophagus passes from the head into the thorax and widens there into a more or less spacious crop generally extending throughout the greater part of the thoracic length, often well into the abdomen. The proventriculus is usually a distinct chamber with thickened muscular walls and a specialized cuticular lining, but may be little more than the stomodaeal or cardiac valve, and may be indistinguishable in external view.

The mid-gut is a cylindrical tube, usually shorter than the fore-gut, generally straight or nearly so, and of about uniform caliber, more rarely curved or even forming a complete loop. At the anterior end its wall is generally produced into two or more diverticula, the *gastric caeca*, but these are not always present. The mid-gut terminates in a slight valvular constriction, the pyloric valve, and is followed by the intestine, which is divided into two regions, the anterior and posterior intestines. The anterior intestine may be straight and axial or it may exhibit various degrees of curvature, being sometimes distinctly convoluted. It is often divided into two regions of different caliber, the more dilated part being sometimes anterior, sometimes posterior, or there may be three divisions, the dilated part being the middle one. The hind intestine, commonly known as the rectum, is generally an ovoid chamber and contains six epithelial cushions, the rectal pads or rectal glands. Malphigian vessels are always present, opening into the anterior intestine immediately behind the pyloric valve. They vary greatly in number and arrangement, being sometimes distributed uniformly, sometimes in groups, each group with a common duct, or, in extreme cases, there may be a single common duct for all of the vessels.

The salivary or labial glands in orthopteroid insects are much divided, paired structures, lying in the thorax chiefly in the region of the oesophagus, the ducts from each glandular mass uniting below the digestive tube to form a common duct, which opens on the ventral wall of the head between the labium and the hypopharynx. In most forms there are paired salivary reservoirs, which are large diverticula of the salivary ducts, usually the paired ducts, but sometimes of the common duct.

In this section the digestive organs of *Grylloblatta* are compared with published descriptions of these organs in the following orthopteroid groups:—

Order	*Family*
Dermaptera	Forficulidae
Plecoptera	Pteronarcidae, Perlidae, Nemouridae
Blattodea	Blattidae
Mantodea	Mantidae
Isoptera	Hodotermitidae, Termitidae
Phasmida	Phasmidae
Saltatoria	
Suborder Caelifera	Acrididae, Tetrigidae, Tridactylidae, Cylindrachetidae
Suborder Ensifera	Tettigoniidae, Gryllacrididae, Rhaphidophoridae, Stenopelmatidae, Gryllidae, Gryllotalpidae.

Dermaptera

In general plan the digestive tube of *Grylloblatta* is not unlike that of *Forficula auricularia* L. as described and figured by Bordas (5).

Features common to these forms are:

(1) The course of the tube is for the most part straight, having only a slight to moderate convolution in the region of the stomach and intestine.

(2) The external divisions are the same, viz., *fore-gut*—pharynx, oesophagus, crop, proventriculus; *mid-gut*—ventriculus or stomach; *hind-gut*—anterior intestine, posterior intestine or rectum.

(3) The relatively short hind-gut, of which the anterior part (anterior intestine) is not divided into ileum and colon.

(4) The somewhat feeble cuticular armature of the proventriculus, which in neither form could be used for triturating the food.

(5) The relatively small number of malpighian vessels (smaller in *Forficula*).

(6) The alternate arrangement of the six rectal pads.

The differences are more striking. The more important of these may be listed as follows:

(1) The relatively small crop in *Forficula*, which according to Bordas' figure, is smaller than the mid-gut, whereas in *Grylloblatta* it is very much larger.

(2) Differences in the proventriculus:— absence in *Forficula* of the collum which is unusually well developed in *Grylloblatta*; internal lamellae in *Forficula* six instead of 12 as in *Grylloblatta*, their forward projections into the terminal part of the crop and their backward extensions into the mid-gut in the form of six long valvular processes having no counterpart in *Grylloblatta*.

(3) The much larger ventriculus in *Forficula*, with *no trace of gastric caeca*.

(4) The grouping of the malpighian vessels in *Forficula* into two fascicles, in contrast to their even distribution around the pylorus in *Grylloblatta*.

PLECOPTERA

In the few genera of stone-flies in which the digestive organs have been studied there appear to be wide variations in several directions.

In the primitive genus *Pteronarcys*, according to Newport (38), the oesophagus gradually widens into a crop that extends through the thorax into the abdomen as far as the fourth segment. Although Newport makes no mention of a proventriculus and there is no indication of one in his figure, it is probably developed to some degree in the nymph. There are no gastric caeca but the ventriculus is remarkably long and convoluted, extending posteriorly to the ninth abdominal segment, where it meets the extremely short intestine. The latter is divided into two sections designated ileum and colon by Newport, but doubtless the anterior and posterior intestine, according to our terminology. The malpighian vessels number 40 to 50 and appear in Newport's figure to be evenly distributed around the pylorus.

Nemoura vallicularia, investigated by Wu (59), and *Perla* by Schoenemund (47) and Imhof,* both differ from *Pteronarcys* in the straight course of the alimentary canal. *Nemoura* resembles *Pteronarcys* in the lack of gastric caeca and in the very long ventriculus, which extends from the prothorax to the end of the fourth abdominal segment. It is unlike *Pteronarcys* in the very short stomodaeum, which terminates in the prothorax, instead of passing halfway through the abdomen. The expanded posterior part, termed by Wu the proventriculus, is evidently the crop.

In *Perla*, there is again a very large crop, extending well into the abdomen. The nymphal proventriculus has been studied by Schoenemund (47) and that of the related genus *Acroneuria* by Judd (33). It is cylindrical and but slightly marked off externally from the crop. The inner lining in both of these genera is unlike that of most orthopteroid insects but resembles that of *Grylloblatta* slightly in that there are, over a part of its area, 12 similar divisions, i.e., longitudinal folds or ridges, instead of six, which is the usual number in orthopteroid insects. The ventriculus is much shorter than in *Pteronarcys* and *Nemoura* but there is a circle of forwardly directed gastric caeca, which are slender and conical like those of the Acridoidea. There are eight of these according to Schoenemund, 10 according to Imhof, and seven in Acroneuria (Judd, 33). In all of these forms there are two lateral caeca which are longer than the others. The gastric caeca are present in the adult stage as well as the nymph (Schoenemund, 47).

The intestine is short in all of the plecopteran genera described and in each form it pursues a straight course. The anterior intestine ("colon") of *Perla* sp.,

* *According to Imms (32) and Weber (57).*

is described by Schoenemund as opening into the rectum somewhat asymmetrically, and in the same genus (according to the generic concept of the period), Newport (38) describes and figures a distinct caecum arising from the rectum ("colon"). The malpighian vessels vary from 36 in Nemoura to about 80 in *Perla*. They appear to be arranged usually in a simple circle in the forms described.

Grylloblatta resembles all the plecopteran genera described here in the division of the intestine into two regions only, and in the simple arrangement of the malpighian vessels. It is like *Pteronarcys* and *Perla* in the long oesophagus and crop, extending into the abdomen, and it is somewhat like *Perla* in the short wide ventriculus. It also resembles *Perla* and *Acroneuria* slightly in the inner structures of the proventriculus, the lining epithelium and cuticle, over a part of its area, being raised into 12 similar longitudinal folds or ridges instead of the usual six.

Grylloblatta differs from the Plecoptera in the form of its very muscular proventriculus with collum and bulb, in the number and very different form of the gastric caeca and in the longer and somewhat convolute intestine. In general the alimentary canal of the Plecoptera is more like that of the Caelifera than that of *Grylloblatta*.

Blattodea

The organs of digestion in the cockroaches have been described by a number of authors, e.g. Miall and Denny (37), Bordas (6, 9), and Petrunkewitsch (39). Most of the work, however, has been done on the two common and nearly related forms *Blatta orientalis* and *Periplaneta americana*, but Bordas gives general descriptions of a number of genera. In these there is considerable variation, but the common plan of structure is the same.

With the Blattodea *Grylloblatta* shares the general features of the digestive system as already outlined, including a thick-walled proventriculus visible in external view, a mid-gut with at least the beginnings of gastric caeca, and an intestine that has at least one flexure. *Grylloblatta*, however, differs strikingly from the Blattodea in certain respects, viz.:

(1) The presence of a muscular tube or collum between the crop and the bulb of the proventriculus.

(2) The very different structure of the cuticular intima of the proventriculus the parts of which are arranged on a plan of 12 similar divisions instead of six and are quite different in detail from those of any of the Blattodea, so far as known (*vide* Judd, 33).

(3) The much shorter mid-gut with the broad incipient pair of gastric caeca, instead of the eight slender tubules of the Blattodea.

(4) The much shorter hind-gut of which the first section or "anterior intestine" has no subdivisions such as are found in the Blattodea.

(5) The fewer malpighian vessels, arranged in a circle, with independent openings, in place of the numerous tubules in the Blattodea divided into six groups, each having an opening into a conical elevation of the intestinal wall.

(6) The more compact salivary glands whose main ducts lack the usual salivary reservoirs, which are present in the Blattodea.

Mantodea

In the digestive system as in all the organ systems the Mantodea give evidence of near relationship to the Blattodea. The chief differences lie in the greatly elongated oesophagus, the inner structure of the proventriculus (Judd, 33), the shorter mid-gut, the usually shorter and less convoluted hind-gut, the anterior intestine not being subdivided as in the Blattodea, and the simple arrangement of the malpighian vessels, which are not grouped, each having its independent opening into the anterior end of the intestine.

Grylloblatta resembles the Mantodea in the same features as indicated for the Blattodea and, further, in the shorter mid-gut, less convoluted anterior intestine, lacking division into two distinct regions, and the simple arrangement of the malpighian vessels, which however, are fewer than in the Mantodea. The greater resemblance of *Grylloblatta* to the Mantodea than to the Blattodea, however, has probably no phylogenetic significance.

Isoptera

The digestive organs of the termites have been investigated by Holmgren (30), Imms (31), Sutherland (49), and others, and a good general account of them is given by Imms (32). The organs are not unlike those of the Blattodea, particularly in the more primitive genera (Hodotermitidae). This similarity is seen, e.g., in the conical proventriculus with its broad base connected with the crop, the elongation and curvature of the ventriculus, which often completely encircles the intestine, and the division of the anterior intestine into at least two sections, the ileum being separated from the colon by a spiny zone, considered by Imms to be a valve ("pyloric valve"), but termed by Sutherland the "posterior gizzard" and believed by her to "grind any larger particles of food which have been left over by the anterior gizzard before they enter the large intestine" (colon).

Holmgren points out that in primitive termites such as *Hodotermes* the crop is a large sac, as in the *Blattodea*, but in most of the genera it is reduced and restricted to the abdomen, while the oesophagus is greatly elongated and the proventriculus tends to be larger than in primitive genera. A specialized feature of the proventriculus of most Isoptera is a more or less pronounced neck or *collum* between the bulb and the ventriculus. Judd (33), who describes the proventriculus of *Termopsis*, states that "its inner lining resembles more closely that of the Blattodea than of the Mantodea as it has longitudinal folds rather than anastomosing ridges between the teeth".

In the numerous genera described by Holmgren there are no true gastric caeca, but in the primitive genus *Archotermopsis* there are five short diverticula at the anterior end of the stomach (Imms, 31). Sutherland, who investigated the anatomy and histology of a number of Australian termites, including the very primitive *Mastotermes*, makes no mention of gastric caeca in that genus.

In all these structures and also in the intima of the proventriculus, *Grylloblatta* differs from both Isoptera and Blattodea. The proventriculus is narrowed into a neck in front of the bulb but not behind, the ventriculus is short and wide and there are only two incipient gastric caeca which are broadly rounded. The intestine is much shorter than in the Isoptera and the anterior part is simple. The malpighian vessels are more numerous than in the Isoptera, in which there are not more than eight and frequently only four or two. Even when only four are present they are grouped into two pairs, while in *Grylloblatta* they are about equally spaced.

Phasmida

The digestive organs in this order have been described by Bordas (7, 11), who investigated various genera, and by Heymons (27) and Cameron (13), who made more detailed studies of *Bacillus rossii* Fabr.

The alimentary canal in this order differs considerably from those of other orthopteroid insects in a combination of features, some of which are unique. Its most striking peculiarities are the following:—

(1) The straight course of the entire tube.

(2) The relative short and narrow crop.

(3) The thin-walled and ill-defined proventriculus.

(4) The elongation of the mid-gut and its division into two specialized regions, the anterior characterized by well developed circular muscles arranged in annular bundles and associated with a pronounced transverse folding of the walls, while the posterior region is thinner-walled and is characterized by the presence of tubular filiform organs.

(5) The absence or rudimentary development of gastric caeca.

(6) The numerous malpighian vessels grouped into a number of small bundles, each opening into the summit of a small conical papilla.

In the lack, or feeble development, of gastric caeca, the Phasmida resemble the Dermaptera, while in the straight course of the digestive tube and the absence of a definite thick-walled proventriculus they are like the Plecoptera and the suborder Caelifera of the Orthoptera.

Saltatoria

The order Saltatoria consists of two very distinct suborders, the *Caelifera* and the *Ensifera*. The digestive system in these two suborders is so different

as to suggest that the Saltatoria may not be an entirely natural order (*vide* Discussion). It will, therefore, be convenient to consider these two groups separately.

The suborder Caelifera includes two superfamilies *Acridoidea* and *Tridactyloidea*, the close affinity of which has only comparatively recently been thoroughly cleared up by the work of Carpentier (16, 17) and Ander (1, 2).

Of the four families of Acridoidea, the Acrididae comprise the great majority of all the Caelifera. In this family the digestive systems of many species, representing five of the subfamilies, have been described by Bordas (10, 11), and more recently a number of additional forms have been brought to light by several workers, e.g., Tietz (51) and Hodge (28, 29). The range of variation among these forms is remarkably slight and the differences from our point of view are negligible.

The salivary glands in the Acrididae tend to be reduced and diffuse, and the reservoirs are inconstant, being sometimes absent. The alimentary canal is straight or nearly so, the oesophagus is rather short and the crop well developed but not very voluminous. The proventriculus is not externally apparent, being tubular without thickening of the muscular coat and with very little specialization of the epithelial and cuticular lining. The ventriculus is straight, cylindrical, and usually rather short and wide. There are six conical gastric caeca, directed forward, each with a posterior diverticulum applied to the surface of the ventriculus.

The anterior intestine is sometimes straight and of nearly uniform caliber, but it is more often divided into a broader anterior part, which is straight, and a constricted posterior part, which is often bent downwards in the sagittal plane. The malpighian vessels are long and numerous, numbering commonly 100 to 120, although sometimes only 30 to 40 (Bordas, 11). They are generally more or less distinctly grouped into fascicles, some of which are directed forward and others backward.

The alimentary canal of *Tetrix* (*Acrydium*), representing the family Tetrigidae, was first made known by Dufour (20) and has recently been described by Carpentier (16, 17). It differs from that of the Acrididae in the very short oesophagus and crop, the relatively much longer ventriculus, and the absence of the posterior diverticula from the six fingerlike gastric caeca. There are a dozen groups of malpighian vessels. The presence of two large salivary reservoirs also differentiates *Tetrix* from most of the Acrididae.

The other two families, Proscopidae and Pneumoridae, have not been studied.

The digestive organs of the Tridactylidae were first described briefly by Dufour (20), who studied *Tridactylus variegatus*. He noted their similarity to those of *Tetrix* and was the first to cast doubt upon the accepted classification of this genus among the Gryllidae. Nearly a century later Carpentier

(16) described and figured the gross features of the digestive organs of *T. thoracicus* and demonstrated the similar plan of structure of these organs in the Tridactylidae, Cylindrachetidae, and Tetrigidae.

The oesophagus and crop are even shorter in *Tridactylus* then in *Tetrix*, the crop being also very little inflated. The ventriculus, like that of *Tetrix*, is the longest section of the digestive tube and the largest in caliber. In *T. thoracicus* it is produced cephalad into four conical gastric caeca (Carpentier, 16), in *T. variegatus* (Dufour, 20; Fernando, 24) there are three, two larger dorsolateral and one smaller midventral, while Judd (33) found only the two lateral ones in *T. apicialis*. This number was also noted by Ander in the tridactylid genus *Rhipipteryx*. The intestine is straight and its divisions are similar to those usually found in the Acridoidea. Fernando describes the 32 malpighian vessels in *T. variegatus* as being arranged in a simple circle, not in tufts as described by Carpentier for *T. thoracicus*. He also differs from Dufour in his statement that the salivary glands are without reservoirs, since these are distinctly shown in Dufour's figure of the same species.

Cylindroryctes, of the family Cylindrachetidae, resembles *Tetrix* in having six slender gastric caeca, directed forward and having no posterior diverticula (Carpentier, 16). It differs from all the other groups in the extremely long and slender oesophagus and comparatively long, although little inflated, crop. This difference, however, is what would be expected from the greatly elongated thorax, associated with the habit of burrowing into plant tissues. The ventriculus measures more than half of the length of the abdomen and, as in *Tetrix* and *Tridactylus*, is the largest in caliber of any part of the alimentary canal. The intestine is only about half as long and appears in Carpentier's figure to be about equally divided into anterior intestine and rectum. There are numerous malpighian tubules in many groups, but the exact number is unknown.

The common characteristics of the alimentary canal in the Caelifera may thus be summarized as follows: The salivary glands tend to be diffuse. The alimentary canal is straight or nearly so. The crop is not voluminous, sometimes very small, and the proventriculus is "comparatively simple in structure, being tubular in shape and having no heavy armature in the interior" (Judd, 33). The ventriculus is straight and of large caliber and the gastric caeca, which are typically six but may be reduced to 4, 3, or 2, are always slender and conical. The anterior intestine is short and straight, or only slightly bent, and is usually constricted just before the rectum. The malpighian vessels are numerous and generally grouped into six or 12 tufts.

The suborder Ensifera comprises the two superfamilies Tettigonioidea and Grylloidea. Six families have been recognized in the Tettigonioidea by recent workers and two in the Grylloidea.

Of the six tettigonioid families, by far the largest and most varied is the Tettigoniidae. In this family the digestive organs of a large series of forms were studied by Bordas (11), the proventriculus in particular by Graber (25),

Ramme (41, 42), Wilde (58), and Judd (33), while the features that are important from the comparative standpoint of this and other families of Ensifera have been described by Ander (2).

The alimentary canal in the Tettigoniidae is long and convoluted. The oesophagus is usually short but the crop is large, often extending into the abdomen, and usually widest near the posterior end. According to Ander (2) it is much more inflated dorsally than ventrally, and this is characteristic of the Tettigonioidea in general. The proventriculus is a muscular bulb connected with the crop by a very short collum, which is merely a connecting passage with sphincter function. The intima is elaborated into a complex armature consisting of (*a*) six longitudinal columns of sclerites, each including a median and two lateral teeth, and flanked by a series of "barbated lobes", and (*b*) an alternating series of six longitudinal sclerotized ridges. The proventriculus is constricted again at its junction with the ventriculus, into which it opens by the stomodaeal valve. The valve is generally prolonged into two large free flaps, dorsal and ventral, projecting freely into the ventricular cavity. The proventriculus is embraced, and often largely concealed, by the two broadly rounded gastric caeca. These are slightly displaced, the dorsal caecum leaning to the right (Ander, 2). The lining epithelium is folded into parallel lamellae of varying height, which serve to increase the secretory surface and divide the cavity of the caecum, partially or (rarely) completely, into a number of chambers. In certain Pseudophyllinae and Mecopodinae (Bordas, 11; Karny, 34) each caecum has a slender posterior diverticulum, somewhat reminiscent of those found in the Acrididae, but undoubtedly this is a specialized feature (Ander, 2).

The ventriculus is a long tube, sometimes twice as long as the body, and more or less convoluted, sometimes forming a single loop, sometimes three or four. It is not divided into specialized regions and is either uniform in caliber or somewhat broader in front, where the caeca open into it. The intestine is generally shorter but the anterior part is sinuous or somewhat convoluted, although not further subdivided. The rectal sac is variable in size but is an ovoid chamber with six strong bundles of longitudinal muscles and six rectal glands, radially arranged at equal distances. The malpighian vessels, generally numerous (100 to 120), are typically grouped in six clusters, each cluster discharging into the intestine through one of the six ampullae. These may be evenly spaced or grouped in three pairs. Sometimes the number of ampullae is reduced to three or four, or the vessels themselves are not definitely grouped but irregularly arranged.

The salivary glands in the Tettigoniidae are generally voluminous, often covering the whole ventral surface of the thoracic floor and encroaching upon the sides and dorsal surface of the crop. They are usually divided into two sections, a smaller one in front and a larger behind. In *Salomona* (Bordas, 11) the salivary glands are compact and lie in contact with one another on the

dorsal surface of the oesophagus and base of the crop, a position recalling that of *Grylloblatta*. Salivary reservoirs are usually present but are not seen in Bordas' figure of *Salomona*.

The digestive system of the Stenopelmatidae has been studied in *Hemideina* (Maskell, 36) and in *Stenopelmatus* (Davis, 18). The salivary glands are not very voluminous in either genus, although the reservoirs are well developed. The alimentary canal does not differ from that of the Tettigoniidae in any important respect. There is no definite collum between crop and proventriculus, the lining of which is very similar to that of the Tettigoniidae. The gastric caeca may or may not have low lamellae (absent in *Hemideina*) and the free flaps of the stomodaeal valve are as in the Tettigoniidae. The ventriculus is shorter than in the latter family, particularly in *Hemideina*, while the anterior intestine in this genus is much longer and has a short section of narrow caliber, termed by Maskell the "ileum", followed by a long expanded section, called the "colon", and the constriction just before the rectum is unusually long. In *Stenopelmatus*, however, the intestine is much shorter and quite like that of the Tettigoniidae. The widest part, termed "colon" by Maskell, is the "ileum" of Davis, who applies the term "colon" to the constricted region just in front of the rectum. The malpighian vessels are divided in the typical tettigoniid fashion in six equidistant groups, discharging through as many ampullae, into the intestine. There are about 200 tubules in *Hemideina* while in *Stenopelmatus* they were found to vary from 180 to over 300.

In the Rhaphidophoridae noteworthy features are —: the relatively short ventriculus, which is expanded anteriorly into a sort of vestibule for the broadly rounded gastric caeca, whose inner lining is devoid of lamellae; the presence of three equidistant free lobes of the stomodaeal valves, projecting into the caeca; and the reduction of the ampullae of the malpighian vessels to four, three, or only two. The writer found only two in *Ceuthophilus pallidipes*, close together on the inner curvature of the intestine.

In the Gryllacrididae the crop, according to Ander (2), is large, bulging posteriorly, and is sharply defined from the rather long proventricular collum. Bordas (11) depicts these features in his figure of "*Gryllacris aurantiaca*". Karny (34), however, describes the crop of *G. signifera* as more "primitive" and less like a caecum than in the Gryllidae and in his figures it appears decidedly small and without any posterior bulging, tapering in fact to its junction with the collum.

The gastric caeca are large in the Gryllacrididae, while the ventriculus is decidedly short for a family of Ensifera. In Bordas' figure cited above, all the malpighian vessels empty into a single ampulla, and this character, together with the posteriorly inflated crop and the long collum joined to it asymmetrically, was believed by Bordas to indicate affinities between the Gryllacrididae and the Gryllidae. Ander, however, dissected a number of

species of Gryllacrididae and found the single ampulla to be exceptional in this family, the majority of species observed having six, the usual number in the Tettigonioidea.

According to Ander the Schizodactylidae share with certain Gryllacrididae the posteriorly inflated crop and the comparatively long collum, and in both families the cavities of the gastric caeca are partially divided into chambers by two to seven lamellae, although in *Schizodactylus* the five chambers are almost complete. In this genus there are the usual six ampullae through which the malpighian vessels discharge into the pylorus.

One other family, the Prophalangopsidae, belongs to the Tettigonioidea, but it is represented with certainty by only the type genus *Prophalangopsis* with one species, *P. obscura* Walk., whose internal anatomy is unknown. The genus *Cyphoderris*, referred to this family by Zeuner (60), appears to be near the Stenopelmatidae and Tettigoniidae in the characters of the alimentary canal, including the minute structure of the proventriculus (Ander, 2).

The superfamily Grylloidea is similar to the Tettigonioidea in the general structure of the digestive organs but there are a few special characteristics, which may be listed as follows:

(1) According to Ander (2) the crop is generally expanded ventrally instead of dorsally, and the stomodaeum is twisted from left to right, so that the expanded part of the crop lies on the left side and the gastric caeca may be swung into a more or less lateral position.

(2) There are four main lobes in the stomodaeal valve, all usually small and none in the primary sagittal plane.

(3) Differences in the armature of the proventriculus, which need not be specified here (*vide* Ander, 2; Judd, 35).

(4) The ventriculus is divided into two distinct regions, separated by a sphincter muscle, an anterior region, which is smooth both externally and internally, and a posterior region longer and of larger caliber, with an uneven outer surface bearing three rows of small evaginations, and an inner surface bearing short papilliform processes (Bordas, 12; Ander, 2).

(5) The malpighian vessels open into a single ampulla at the summit of a common duct or ureter, which discharges into the pylorus.

In the family Gryllidae the oesophagus passes gradually into the crop, the shape of which is not very different from that of the Tettigonioidea except in the usually ventral expansion and the more or less asymmetrical opening into the proventriculus which is somewhat in advance of the posterior end, on the right (ventral) side. There is a distinct although usually short collum proventriculi: the cavities of the gastric caeca are incompletely divided by low epithelial lamellae. The ventriculus is typically long and convoluted although short and wide in *Myrmecophila* (Schimmer, 46), which lacks the usual division into two regions. The intestine is shorter than the ventriculus and does not differ significantly from that of the Tettigonioidea.

The Gryllotalpidae, which have been studied by Bordas (11), Eberli (22), and Sayce (45), possess, in addition to the special grylloid features, a few of their own, viz:—

(1) The oesophagus is long, of uniform diameter, and opens abruptly into the crop.

(2) The expansion of the crop is mainly perpendicular to the general axis of the digestive tube, so that the organ appears like a caecum.

(3) The crop narrows again abruptly into a tube which is continued into the well marked collum proventriculi.

(4) A pair of "arborescent glands" open into the ventriculus close behind the openings of the two caeca.

(5) The peculiar structure of the posterior region of the ventriculus is continued into the anterior intestine.

The common characters of the Ensifera, excluding highly specialized features, may be summarized as follows:—

Salivary glands voluminous with large reservoirs: oesophagus gradually enlarging into an ample crop, which extends usually through the thorax, often into the abdomen, and reaches its greatest diameter near the posterior end. Proventriculus a muscular ovoid chamber, often with a short neck or "collum" connecting it with the crop, and with a highly developed cuticular armature arranged on a plan of six longitudinal columns of dentiferous sclerites, alternating with sclerotized ridges, the general plan subject to innumerable variations of taxonomic value. The proventriculus is constricted again at its junction with the ventriculus, into which project a small number of free flaps from the stomodaeal valve, the number and arrangement of which is more or less characteristic of the various families and subfamilies. Proventriculus embraced by the two broad, rounded gastric caeca, which are primarily dorsal and ventral, but are generally more or less twisted from left to right so that they assume an oblique or even transverse position; their cavities usually incompletely divided into a small series of chambers by parallel lamellae, formed by folding of the lining epithelium. Ventriculus generally a long and more or less convoluted tube; malpighian vessels commonly divided into tufts, each opening into one of the six, or fewer, ampullae, which open into the pylorus: intestine shorter than ventriculus, but not straight, the rectum ovoid and often large.

From the foregoing descriptions of the digestive organs of the two suborders of Saltatoria, Caelifera and Ensifera, we may make the following comparisons with *Grylloblatta*.

(1) In the Caelifera the salivary glands are usually diffuse and sometimes scanty; in the Ensifera they are generally voluminous, each set divided into two groups of glands. In *Grylloblatta* the glandular masses are more compact than in either suborder of Saltatoria and embrace the oesophagus more closely. The absence of salivary reservoirs has no comparative significance.

(2) The crop is usually small to moderate in size in the Caelifera, voluminous often extending well into the abdomen, and widest near the posterior end in the Ensifera and in *Grylloblatta*.

(3) The proventriculus in the Caelifera is tubular, indistinguishable externally, without thickened muscular walls and with very little specialization of the lining epithelium and cuticle. In both Ensifera and *Grylloblatta* it is ovoid with thick muscular walls, sometimes connected with the crop by a "collum" which is best developed in *Grylloblatta*. In the Ensifera it is lined by a specialized armature of dentiferous sclerites arranged in six longitudinal series, alternating with ridges, while in *Grylloblatta* there are 12 rows of backwardly directed lamellae, which are not firmly sclerotized.

(4) The gastric caeca in the Caelifera are slender and conical; there are primarily six but they may be reduced in number, sometimes to two, which are lateral. In the Ensifera and *Grylloblatta* there are two broadly rounded caeca, embracing the posterior part of the proventriculus. In the Ensifera they are said to lie in the primary sagittal plane: in *Grylloblatta* they appear to be lateral and ventrally confluent.

(5) The ventriculus is straight in the Caelifera, of large caliber, variable in length; in the Ensifera generally much longer, often much exceeding the body length, more slender, and convoluted or, when relatively short, at least curved; in *Grylloblatta*, very short but forming part of a convolution; widest in front, as in many Ensifera.

(6) Malpighian vessels vary in the Caelifera from about 30 to at least 120, in the Ensifera from 100 to 300, and in both groups they are typically divided into six fascicles, each discharging into the intestine through an ampulla. In a few cases, when the vessels are not numerous, e.g. *Tridactylus variegatus* (Caelifera) they open individually into the intestine. This is also the case in *Grylloblatta* in which there are less than 30 vessels.

(7) The intestine in the Caelifera is short and straight or nearly so; in the Ensifera longer and more or less looped or convoluted; of moderate length in *Grylloblatta*, the rectum being large and the anterior intestine very short and twisted similarly to that of some of the more primitive Ensifera; musculature feebler than in the Saltatoria.

It is evident from the above comparisons that *Grylloblatta* has much more affinity with the Ensifera than the Caelifera, in respect of the digestive organs, and closer affinity with this group than with any other group of orthopteroid insects that we have considered. In fact the external appearance of these organs compares closely with those of the Ensifera, the chief differences being the more compact salivary glands, the long *collum proventriculi* and the short ventriculus. If the gastric caeca are truly lateral and those of the Ensifera actually dorsal and ventral, then the case for affinity between *Grylloblatta* and the Ensifera is certainly weakened. Otherwise the greatest difference

lies in the specialization of the inner lining of the proventriculus, which in the Ensifera is generally considered to function as a triturating organ, while in *Grylloblatta* this is obviously not the case.

The question as to which family of Ensifera most nearly approaches *Grylloblatta* is of little moment, since the common ancestor of the Ensifera and Grylloblattaria must have been a form that existed before any of the modern families had yet evolved. This is indicated by the numerous primitive characters still possessed by *Grylloblatta*, such as the cursorial legs, the five-jointed tarsi, the segmented cerci, movable coxites of the male, presence of a metathoracic spinasternite, etc.

As far as the digestive organs are concerned there is little to choose among the families of Ensifera. The short mid-gut and anterior intestine of *Grylloblatta*, perhaps correlated partly with a largely carnivorous diet and partly with the extremely low metabolic rate, is most nearly approached by the Rhaphidophoridae, which resemble *Grylloblatta* in the relatively short ventriculus and anterior intestine and the short, broadly rounded gastric caeca, in which there are no epithelial lamellae. *Grylloblatta* is also somewhat grylloid in the form of the crop, in that the inflation appears to be chiefly ventral and the posterior end is somewhat bulging, and in the long proventricular collum whose junction with the crop is slightly asymmetrical. Some of the Gryllacrididae appear also to share these features with *Grylloblatta*.

The compact salivary glands of *Grylloblatta*, with their lack of reservoirs, and the simple arrangement of the malpighian vessels, are approached to some extent by certain Ensifera, notably *Salomona megacephala* (Bordas, 11), but such features are evidently secondary, as the more scattered form of salivary glands with their well developed reservoirs are general throughout the orthopteroid orders, and the division of the malpighian vessels into tufts, typically six, each discharging into the intestine through an ampulla, is also a general orthopteroid feature.

Discussion

Affinities of Grylloblatta

Comparison of the digestive organs of *Grylloblatta* with those of other orthopteroid groups reveals definite indications of its affinity with the saltatorian suborder Ensifera and with this group only. This is in conformity with our findings in the other papers of this series (Walker, 53-56). *Grylloblatta* differs considerably, however, from any known family of Ensifera in the inner structure of the proventriculus, as well as in many other features referred to in the previous parts of this series. We believe, therefore, that the Grylloblattidae can scarcely be classified as merely a very generalized family of Ensifera, as done by Handlirsch (*vide* Ander, 12), but is worthy of at least subordinal rank. The question then arises as to whether the nearest relatives of the Ensifera are the Caelifera or the Grylloblattaria.

Zeuner (60) claims that the ancestral line of the Ensifera may be traced back to "primitive stenopelmatoid" forms, which are, in part, derived from the family Oedischiidae of the Upper Carboniferous, a protorthopteran family, which possessed jumping hind legs. From the primitive stenopelmatoid forms arose another line which gave rise to the Stenopelmatinae, Gryllacridinae, and also, through the Jurassic family Locustopsidae, to the Caelifera. Thus Zeuner attempts to trace all recent saltatorial groups to saltatorial protorthopteran ancestors (Protosaltatoria).

Ander (2), from the evidence of extensive comparative studies of all the organ systems as well as the skeletal features and musculature, concludes that the Caelifera cannot be derived from the Ensifera and that these two suborders must have evolved independently from different protorthopteran families. He agrees with Zeuner in tracing both lines of descent back at least to the Upper Carboniferous, but differs greatly in the details of their evolutionary history. Such details, however, scarcely affect the systematic position of *Grylloblatta*. The significant point in Ander's conclusions is that he represents the basal stems of the two lines of descent as parallel lines; he does not attempt to trace them to a common ancestor.

Bearing Ander's conclusions in mind, and in consideration of the many features that link *Grylloblatta* with the Ensifera, we venture to suggest that the common ancestor of the Ensifera and Caelifera is to be sought, not in the Protosaltatoria, but in some earlier family of cursorial Protorthoptera, and that the saltatory habit found in both Ensifera and Caelifera must have been independently acquired during the evolution of these two groups, although possibly through the recurrence of the same mutation. *Grylloblatta* would thus be derived from the Ensiferan stock before the saltatory habit had arisen. The Ensifera and Caelifera are thus parallel groups, not only in the possession of saltatory hind legs but also in the reduced number of tarsal joints, and the unsegmented cerci. Evidence that primitive members of both suborders possessed segmented cerci is found in the genus *Speleiacris* of the Ensifera (Ander, 2) and the genera *Tridactylus* and *Rhipipteryx* of the Caelifera, all of which have two-jointed cerci.

This view of the relationship of *Grylloblatta* to the Saltatoria and of the two suborders of the latter to one another differs from that which we have hitherto expressed, in that we were unwilling to admit the dual origin of the saltatory habit and the other parallelisms that are associated with it.

Function of the Proventriculus of Grylloblatta

The most characteristic features of the alimentary canal of *Grylloblatta* appear to be found in the proventriculus, of which the inner structure is strikingly different from that of all other orthopteroid groups and the collum is unusually long and muscular. The great development of the muscle layers of the proventriculus contrasts strongly with the feeble musculature of other parts of the alimentary canal, especially the rectum, whose muscle layers contrast with those of most mandibulate insects, in which they are thickened

for the expulsion of faeces. Some consideration, therefore, of the function of the proventriculus seems to be warranted, even though it is merely deduced from the anatomical findings.

The problem of the function of the proventriculus of insects has been discussed at great length and the published work on the subject has been reviewed from time to time by various authors, such as Rungius (43), Ramme (41), Davis (18), and Deegener (19).

The earlier insect anatomists of the 19th century assumed from its structure that the proventriculus in mandibulate insects functioned as a "gizzard", i.e., an organ for further trituration of the food material after it had been acted upon by the jaws. The complex arrangement of hard toothlike structures lining the cavity of this organ in many insects, and the thick muscular walls, seemed to afford sufficient evidence for this manner of functioning. Such a view is assumed by Dufour (20) and by later authors, such as Graber (25), Wilde (58), and Bordas (11).

Wilde, however, having observed the atrophied condition of the proventriculus in the Acrididae, and the presence of toothlike structures in the anterior part of the crop with thickening of the muscles in this region, believed that in this group the function of the "gizzard", in so far as it existed, was taken over by this modified anterior part of the crop.

While a few workers before the middle of the century cast doubt upon the generally accepted view that the proventriculus of Orthoptera was a gizzard, it was Plateau (40) who exercised the greatest influence on the opinions of later writers. Plateau cites the view of Milne Edwards that the terminal part of the proventriculus was a valve for regulating the movement of food from the crop into the ventriculus, although the anterior part of the organ was a gizzard. Plateau himself claimed that the entire proventriculus functioned only as a regulatory valve and a filter for the food entering the ventriculus. Although his views were based primarily upon observations of adephagous Coleoptera, he extended them to include the Blattodea and the suborder Ensifera of the Orthoptera. He pointed out, e.g., that even in the tettigoniid *Locusta* (now *Phasgonura*) *viridissima*, the vegetable fibers of the food in the proventriculus were found lying in the grooves between the tooth-bearing ridges with their long axes parallel with that of the gut. Plateau denied any triturating function of the proventriculus in either Coleoptera or Orthoptera and, under his influence, this view was widely adopted by a majority of workers, including Petrunkewitsch (39), who experimented with the cockroaches *Blatta* and *Blattella*, and Krüger (35), who worked especially with a pselaphid beetle, *Claviger testaceus*, but applied Plateau's conclusions very generally. Rungius (43) criticized Krüger and others for their generalization that, because the proventriculus functions as a valve and sieve, and is sometimes so degenerate that it could not function as a gizzard, it could therefore never do so. He points out, too, the many outstanding authors who still favor the older view—Bordas (11), Deegener (19), Schimmer (46),

and, above all, Berlese (4). His own work on the proventriculus of *Dytiscus*, which is mainly anatomical, he considered to support the view that this organ is a true gizzard. He thought that this view could be confirmed by examining the crop of a *Dytiscus* just after feeding the insect with meat. The presence in the crop of large coarse pieces of meat just after feeding and the fact that the crop is empty after 24 hr., and the mid-gut contains a fine "brei" showed, in his opinion, that the meat had been ground up by the gizzard into fine particles before being passed on into the mid-gut.

Ramme (41, 42) who made feeding experiments with *Dytiscus*, several Carabidae, and various Orthoptera, agreed with Plateau that the proventriculus does not function as a second triturator of the food but he showed by many experiments that, in all the insects investigated, the gastric secretion is passed forward through the proventriculus into the crop and mixed here with the food, the crop being a more important digestive chamber than had been hitherto realized. Another significant discovery was that in the Dytiscidae and Carabidae the indigestible particles of the food, such as fragments of cuticle, were vomited and never pass through the proventriculus. Ramme's final results were in accord with Plateau's in that he ascribed to the proventriculus only the function of a valve which permits the emptying of the gastric secretion upon the food in the crop and allows the dissolved parts of the food to be strained through into the stomach.

These results, however, are based on the study of Coleoptera and are not necessarily applicable to orthopteroid insects. Eidmann (23) investigated the structure and function of the proventriculus of the cockroach *Periplaneta* (now *Blatta*) *orientalis* and found that the organ was divided into two parts, anterior and posterior. The anterior part contains six radially arranged powerful teeth and is able to comminute hard food particles such as sclerotized cuticle. After comminution the food does not pass immediately into the mid-gut but *re-enters* the crop after some time, in order to be acted upon again by the secretion present there. The posterior part of the proventriculus is chiefly a closing apparatus or valve.

The Ensifera have the most powerful and elaborate system of hard toothlike structures of any group of orthopteroid insects and it is here, if anywhere, that we would expect to find them used as a triturating organ. Du Porte (21) has shown that in *Gryllus* chitinous particles are found in the mid-gut and that they are distinctly smaller than those in the crop. Davis (18) found that a wax pencil introduced into the opening of the proventriculus of *Stenopelmatus*, through a hole in the crop, received an impression of the teeth of the proventriculus.

While the general structure of the alimentary canal of *Grylloblatta* is undoubtedly more like that of the Ensifera than any other group of insects, and even the proventriculus, with its neck and bulb, shares outwardly in this similarity, the internal structure is so different as to indicate some very marked difference in function. Thus, whereas the Ensifera are the group in which the proventriculus most probably functions as a gizzard or triturating organ, that of

Grylloblatta is entirely lacking in anything resembling teeth. Although carnivorous, *Grylloblatta* feeds on soft-bodied insect larvae or ant pupae, and when offered mealworms it devours only the soft parts, rejecting the cuticle. The absence of a molar surface on the mandibles is probably significant in this connection, as is also the absence of a peritrophic membrane, although this feature should not be over-emphasized as it has been observed in only one series of sections. Other features that may be significant in this connection are (1) the large crop and the small stomach, (2) the feeble muscular layers of the alimentary canal, except in the proventriculus, which is decidedly muscular, both in the long neck and the bulb.

The possibility that the proventriculus of *Grylloblatta* may function as a "gizzard" may be eliminated at the outset, owing to the soft nature of the food and the lack of anything resembling teeth in this organ. The lining of the bulb with its double circle of flaps certainly suggests a regulatory valve, but the muscular neck and walls of the bulb, together with the feeble muscle layers elsewhere in the alimentary tract, indicate that the proventriculus may be something more than a mere valve.

Thiel (50) has shown that in certain Coleoptera the proventriculus functions chiefly as a propulsive organ for the food, being the only part of the alimentary canal in which the muscular coat is sufficiently well developed to act in this way. The food material is already in a finely divided, or even emulsified, state. In many Adephaga there are valvular plates in front and behind the chamber of the proventriculus. By peristaltic contractions of the muscular wall of the proventriculus the anterior valve is opened and the chamber is filled with a portion of the crop contents. Next the anterior valve is closed and the posterior valve opened as the contents of the chamber are forced into the stomach. In some Coleoptera the anterior valve is absent, and in *Grylloblatta* the muscular neck would preclude the need of such a valve. It is suggested then that the proventriculus of *Grylloblatta* may function somewhat in the following way. By peristaltic contractions of the muscular collum food is drawn from the crop and passed on to the bulb. While the contracted circular muscles of the proventricular neck close its lumen, the food is expelled from the chamber of the bulb into the stomach. The system of projecting lamellae in the bulb serves to prevent any backflow of the food stream. Since the crop is an important digestive cavity in other orthopteroid insects, it is presumably so also in *Grylloblatta*, the smooth grooves between the bases of the lamellae being apparently fitted for the forward passage of digestive secretions from the stomach, even when the bulb is contracted.

Digestion in *Grylloblatta* is doubtless very slow, since in captivity, at a temperature little above 0° C., it feeds usually only about once in three months. Hence the very thin muscular coat of the intestine may be correlated with the slow movement of undigested food materials along the intestinal tract.

Summary

A. The organs of digestion of *Grylloblatta campodeiformis* Walk. were studied from dissections of adult insects and one series made from a male nymph. The main findings were as follows:

1. The labial or salivary glands are compact and appear throughout most of their length as a single mass surrounding the oesophagus. Salivary reservoirs are lacking.
2. The three main divisions of the alimentary canal are a very large fore-gut or stomodaeum, a very short mid-gut or mesenteron, and a moderately short hind-gut or proctodaeum.
3. The fore-gut is divided into pharynx, oesophagus, crop, and proventriculus.
4. The crop is thin-walled and capacious, not distinctly defined anteriorly but widening posteriorly until it reaches the third or fourth abdominal segment. The inflation is mainly ventral and somewhat sinistral, owing to a slight dextral twist, and the passage into the proventriculus is dorsodextral.
5. The proventriculus is very muscular and consists of a long neck or *collum* and a rounded bulb, terminating in a short stomodaeal valve.
6. The inner lining of the proventriculus is arranged on a plan of 12 instead of the usual six longitudinal divisions. These terminate behind in two alternating series of free, flexible processes, there being no hard, tooth-like structures.
7. The mid-gut consists of one short, wide chamber, the ventriculus or stomach, which is produced forward into a bilobed sac, embracing the bulb of the proventriculus and representing a pair of incipient gastric caeca.
8. There appears to be no peritrophic membrane.
9. The hind-gut is of moderate length and curved into a partial loop. It is divided into the anterior and posterior intestines.
10. The anterior intestine is uniform in caliber and histological structure throughout its length, there being no division into ileum and colon. It is short and forms with the mid-gut a partial loop.
11. The malpighian vessels are moderately numerous (12 to 24) and arranged in a simple annulus around the pylorus, each opening separately.
12. The posterior intestine or rectum is much wider than the anterior and is divided into a wide rectal sac and a narrower rectum proper. The rectal sac contains six rectal pads, arranged alternately.

B. A comparison was made between the gross features of the digestive organs of *Grylloblatta* and representatives of other orthopteroid orders, as described and figured in the literature. The orders represented were Dermaptera, Plecoptera, Blattodea, Mantodea, Isoptera, Phasmida, and Saltatoria (Suborders Caelifera and Ensifera).

C. The affinities of *Grylloblatta* are discussed on the basis of the above comparison of digestive organs with representative orthopteroid groups. The main conclusions are that:

1. *Grylloblatta* shows definite evidence of closer relationship to the suborder Ensifera of the order Saltatoria than with any other orthopteroid group.
2. While *Grylloblatta* resembles the Ensifera in most of the gross features of its digestive organs it differs strikingly in the inner structure of the proventriculus.
3. The differences in the proventriculus together with those already described in other parts of the body are sufficient to warrant its classification in a group apart from the Ensifera, and even from the Saltatoria.
4. The common ancestry of the Ensifera and Caelifera is more remote than that of the Ensifera and Grylloblattaria.

D. The probable function of the proventriculus of *Grylloblatta* is considered on the basis of its peculiar structure. Following a review of the more important papers on the function of the proventriculus in mandibulate insects, it is deduced from the structure of this organ in *Grylloblatta* that it probably functions not only as a regulatory valve but also as a propulsive organ, food being drawn from the crop by the muscular collum and passed into the bulb, whence by contraction of the muscular walls of the bulb it is delivered into the stomach. The very thin muscular layers of the intestine may be correlated with the extremely slow digestion of this insect, associated with the low temperatures at which it is active.

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EXPLANATION OF FIGURES

PLATE I

Grylloblatta campodeiformis Walk., late female nymph, opened dorsally with head removed; general view of viscera, showing alimentary canal in natural position.

FIG. 1. *Right lateral view of a male nymph of Grylloblatta, showing the entire alimentary canal and salivary glands and their positions in relation to the regions of the body and the somites. Semidiagrammatic, based on a study of a series of sections, although no model was constructed. In the living insect the head is prognathous.*

FIG. 2. *Sagittal section of head with pharynx opened. 1, levator muscle of labrum; 6, 7, and 8, dorsal dilators of pharynx; 18, adductor of mandible; 23, adductor of stipes (these muscles are described in Part 1 of this series).*

FIG. 3. *Maxillae and labium with submentum and mentum removed to show the paired salivary ducts embracing the ventral nerve cord and continuing forward beneath the suboesophageal ganglion to the region of the mentun, where they unite to form the common or median duct.*

FIG. 4. *Transverse section through the prothorax, showing the labial or salivary glands, which appear as a single glandular mass overlying the oesophagus, with the prothoracic ganglion beneath it.*

FIG. 5. *Portion of a salivary gland to show the somewhat irregularly shaped acini, composed of large cells with deeply staining, basal nuclei and actively secreting cytoplasm.*

FIG. 6. *Portion of wall of oesophagus, showing the flattened and folded lining epithelium, covered with a thin cuticular intima; also the outer circular muscle fibers and inner longitudinal muscle fibers.*

FIG. 7. *Part of crop, proventriculus, ventriculus and pylorus, with proximal parts of malpighian vessels. Dorsal view.*

FIG. 8. *Entire intestine or proctodaeum, with malpighian vessels and rectal muscles. In the rectal sac the alternating arrangement of the rectal pads shows through the wall of the gut.*

FIG. 9. *Portion of wall of the bulb of the proventriculus, viewed from within, showing eight of the 12 anterior folds (a) and the alternating posterior series (b), which terminate in a row of wedge-shaped processes (c), the second series of processes or lamellae, in alignment with the anterior folds, being alternately longer (d) and shorter (e).*

FIG. 10. *Oblique section through junction of proventriculus and ventriculus, showing the lamellae arising from the epithelial lining of the former, with their cuticular intima, the stomodaeal invagination, and the wall of the ventriculus, the epithelium of which is in an active state of secretion and disintegration.*

FIG. 11. *A portion of the ventricular wall, showing groups of digestive epithelial cells in an active state of secretion, and basal regenerative cells, in a few of which may be seen mitotic figures.*

FIG. 12. *Section through the pyloric region of the wall of the alimentary canal, showing groups of ventricular epithelial cells, epithelium of the anterior intestine, malpighian vessels penetrating the wall of the pylorus and a part of the sphincter muscle (sph).*

FIG. 13. *Transverse section through the anterior intestine, showing folded epithelium and sections of malpighian vessels, the small sections cut near the bases, the larger ones farther distad.*

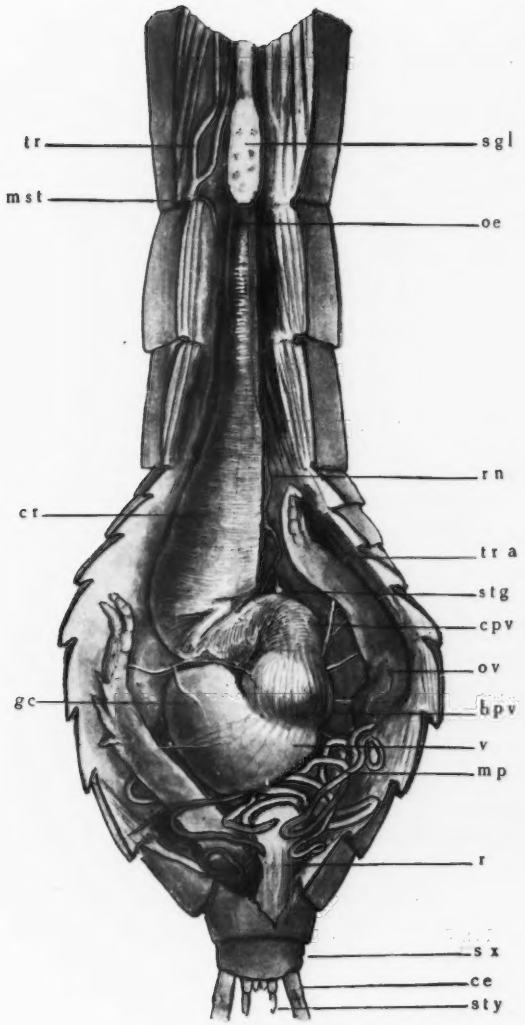
FIG. 14. *Transverse section through part of wall of rectal sac, showing a rectal pad and the extremely flattened epithelium lining the sac elsewhere.*

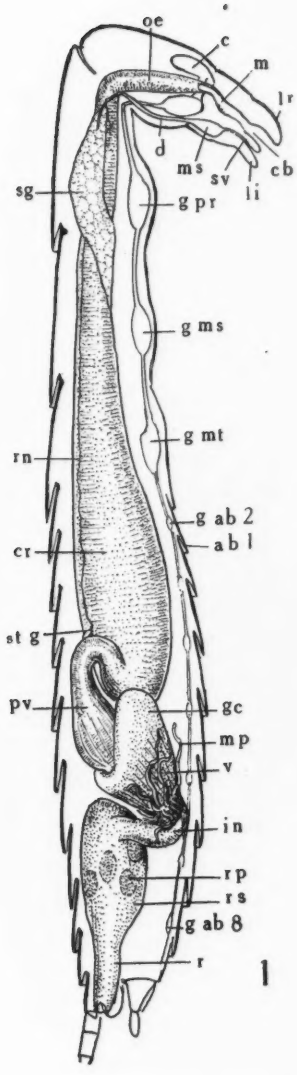
ABBREVIATIONS

bc —*buccal cavity*
bpv —*bulb of proventriculus*
c —*cerebral ganglion*
cb —*cibarium*
ce —*cercus*
cl —*clypeus*
clr —*compressor of labrum*
cpv —*collum of proventriculus*
cr —*crop*
cu —*cuticular intima*
dda —*dorsal dilator of anus*
ddr —*dorsal dilator of rectum*
ep —*epithelium*
epf —*epithelial fold*
ep in—*epithelium of intestine*
ep v —*epithelium of ventriculus*
gc —*gastric caecum*
gl —*glossa*
gms —*mesothoracic ganglion*
gmt —*metathoracic ganglion*
gpr —*prothoracic ganglion*
hy —*hypopharynx*
in —*anterior intestine*
li —*labium*
ln —*labial nerve*
lp —*labial palp*
lr —*labrum*
m —*mouth*
mc —*circular muscle fibers*
md —*mandible*
ml —*longitudinal muscle fibers*
mn —*mentum*
mp —*malpighian vessels*
ms —*median salivary duct*
mxn —*maxillary nerve*
mxp —*maxillary palp*
nc —*nerve cord*
oe —*oesophagus*
ov —*ovary*
ph —*pharynx*
pm —*prementum*
pr —*preoral cavity*
pv —*proventriculus*
r —*rectum proper*
rn —*recurrent nerve*
rp —*rectal pad*
rs —*rectal sac*
rtr —*retractors of rectum*
sd —*paired salivary duct*
sd 1 —*branch of salivary duct*
sgl —*salivary gland*
sm —*submentum*
sog —*suboesophageal ganglion*
sph —*sphincter muscle*
stg —*stomodaeal ganglion*
sti —*stomodaeal invagination*
sty —*stylus*
sv —*salivarium*
tn —*tentorium*
tr —*trachea*
tr a —*trachea from first abdominal spiracle*
v —*ventriculus*
vda —*ventral dilator of anus*
vdr —*ventral dilator of rectum*

(Plate I and Figs. 1–14 follow.)

PLATE I

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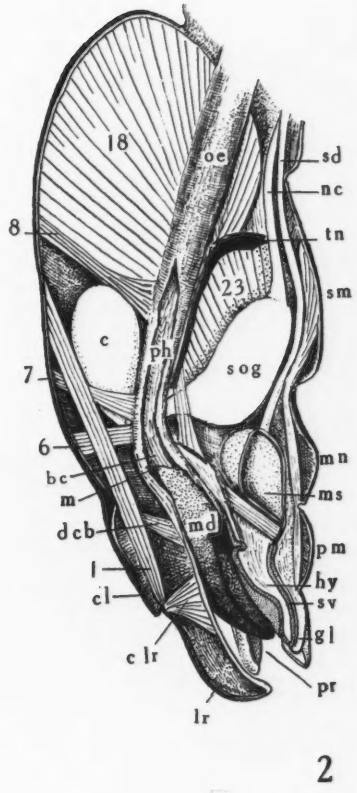
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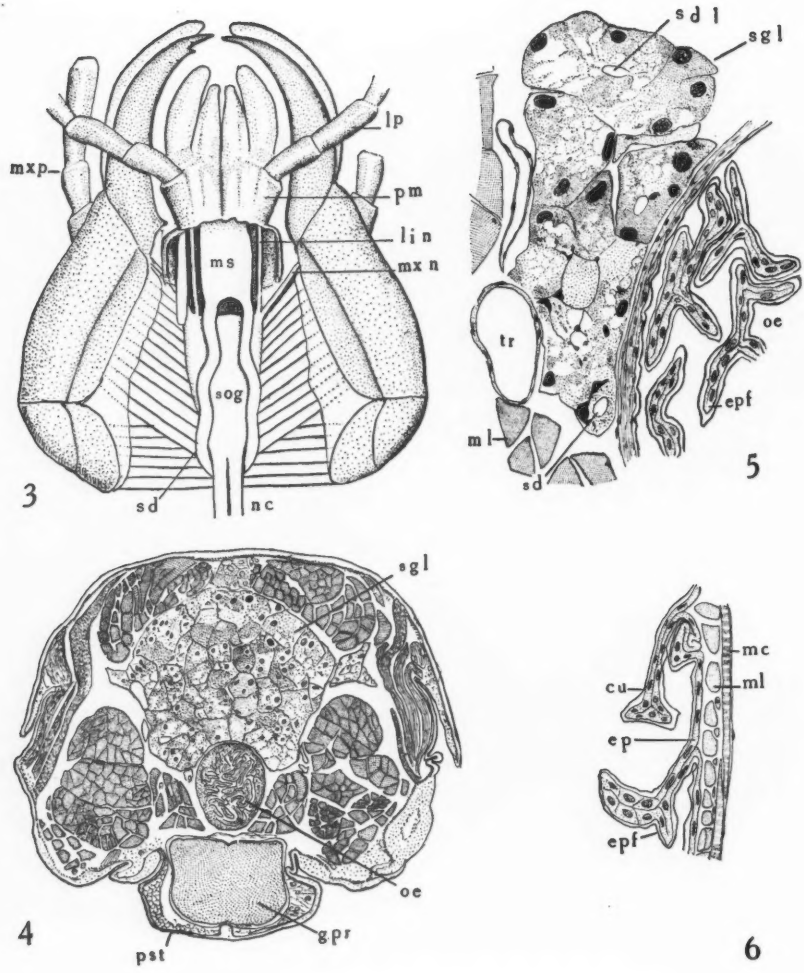
FIGS. 1 AND 2.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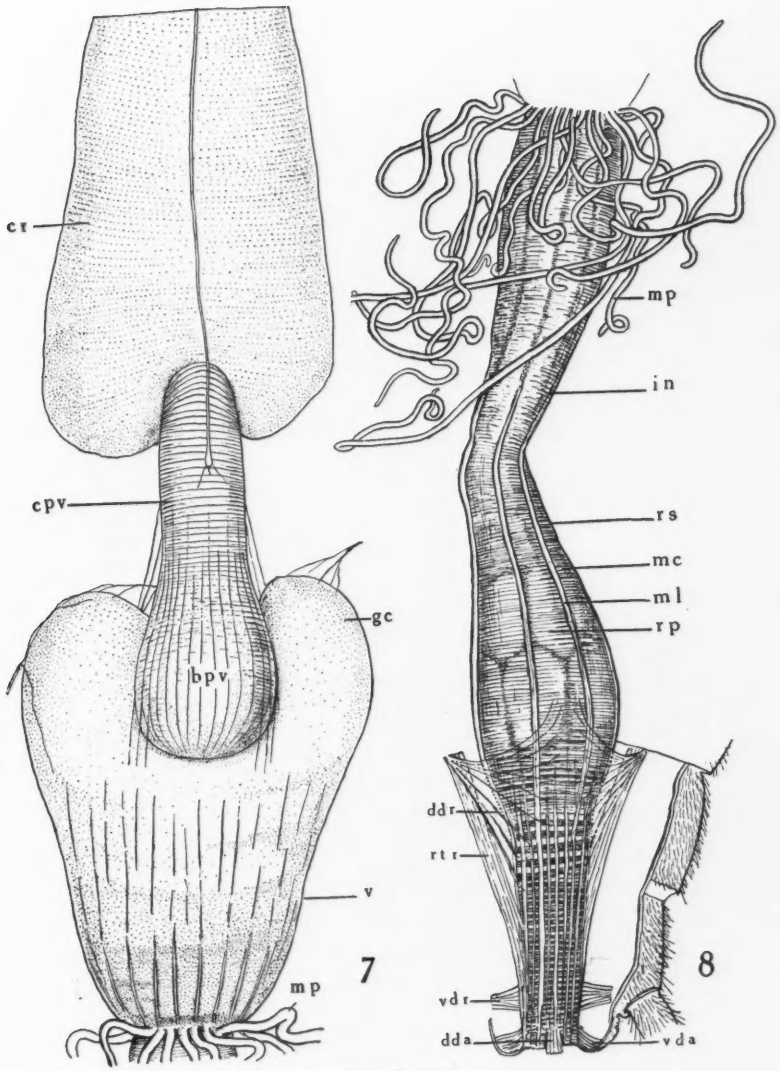
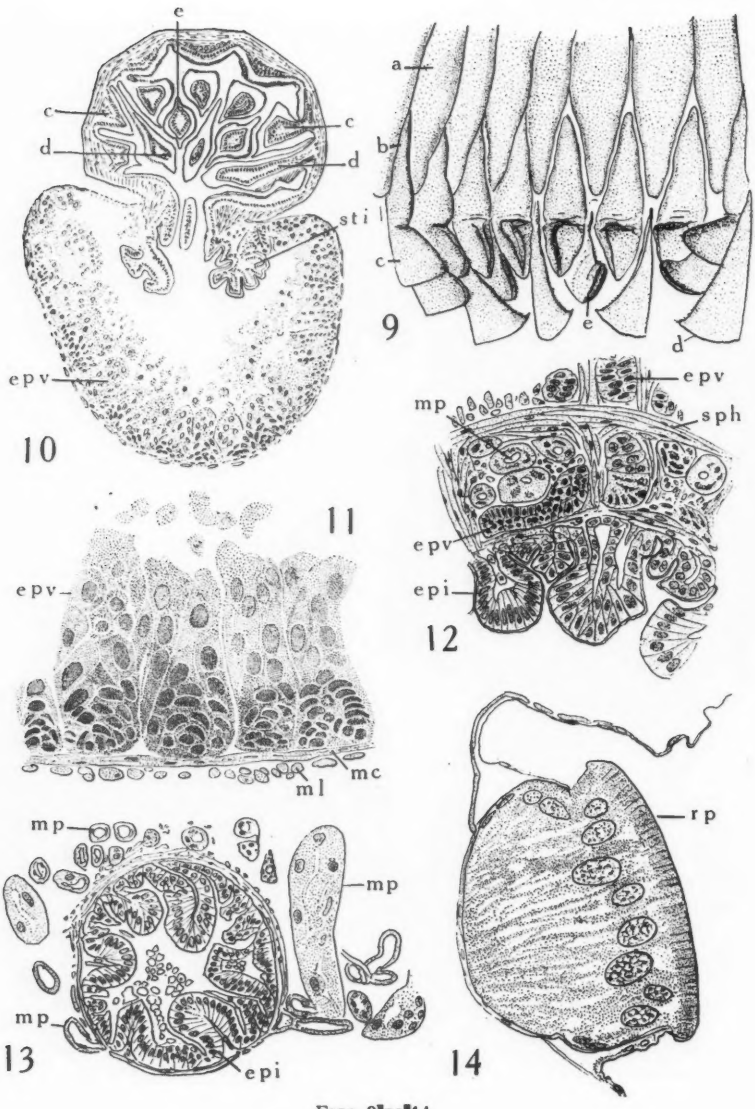
FIGS. 3 TO 6.



FIGS. 7 AND 8.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FIGS. 9 TO 14.

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